

## Keith Roberts Porter: 1912–1997

**K**EITH Roberts Porter died on May 2, 1997, just over a month short of his 85th birthday. He had the perspicacity, good fortune, and patience to take advantage of the fast moving frontier of analytical biology after the Second World War to provide many of the techniques and experimental approaches that established the new field of biomedical research now known as cell biology. He was renowned for taking the first electron micrograph of an intact cell, but his contributions went far beyond that seminal instance. They ranged from technical developments, such as the roller flask for cell culture and the Porter-Blum ultramicrotome, to experimental and observational achievements, such as studies on the synthesis and assembly of collagen, on the role of coated vesicles in endocytosis, on lipid digestion in the intestine, and on the universality of the 9 + 2 axoneme in cilia. The initial ultrastructure descriptions of the endoplasmic reticulum and the sarcoplasmic reticulum, identification of the role of T-tubules in excitation–contraction coupling in muscle and the role of the cytoskeleton in cell transformation and shape change, were his, as were many other contributions, described in some detail elsewhere (Peachey and Brinkley, 1983; Moberg, 1996). Absent from this list are his early pioneering work establishing the androgenetic haploid in frogs, an exercise in nuclear transplantation with consequences for the recent cloning of mammals, and his later adventures with pigment migration in fish chromatophores.

In addition to his specific scientific contributions, Keith Porter also made more important philosophical contributions to the field that he helped to shape. These principles include the understanding that the cell is not a “bag of enzymes”; that organelle structure is consistent from cell to cell throughout a wide range of protists, animals, and plants; that this means that cell structure and function have a macromolecular basis; that self-assembly is a critical morphogenetic principle; and, most presciently, that the cell is structurally integrated down to molecular resolutions by an intricate network of cytoplasmic proteins, this integration having consequences for signal transduction and function. These contributions sometimes involved experienced collaborators and, in later years, young disciples with whom Porter developed particular empathy.

Keith Porter was a boy from Yarmouth, Nova Scotia, who grew up far from the centers of science in the United States and Europe. He went to college at Acadia University in Nova Scotia and then did graduate work at Harvard University. He began his postdoctoral research career at Princeton University and then moved to The Rockefeller Institute for Medical Research (now The Rockefeller University) in the late 1930s, where he joined the laboratory of James B. Murphy. In 1938, he married Elizabeth Lingley, who nurtured him for over a half century. Their family life



Photo courtesy of Dr. Lee D. Peachey.

was disrupted tragically by tuberculosis during the war years, when their young son died. Porter became an American citizen in 1947.

By 1946, Murphy's laboratory included Albert Claude, G.C. Hogeboom, W.C. Schneider, George Palade, who had arrived from Bucharest, and Keith Porter. It was, as Palade described it later, the cradle of cell biology, where cell fractionation and cell fine structure were born and nurtured, and it remained so after Claude returned to Belgium in 1949. In an unusual move, when Murphy retired in 1950, Herbert Gasser, the Director of The Rockefeller Institute, placed Porter in charge of a newly created Laboratory of Cytology and recommended his promotion to Associate Member (equivalent to Associate Professor). Palade also joined this new endeavor, and he became Associate Member in 1953. If Murphy's group nurtured the newborn studies of the cell, the laboratory of Porter and Palade from 1953–1961 raised the field from infancy to maturity.

During these years Keith Porter inspired, created, established, and led the institutions that we know today in the field of cell biology, namely this journal (founded as the *Journal of Biophysical and Biochemical Cytology*) and the American Society for Cell Biology. It is no coincidence that Porter was both the chair of the committee that founded the American Society for Cell Biology and the first editor of the journal, that the *Journal of Cell Biology* is published by The Rockefeller University Press, that the American Society for Cell Biology has played an important role in the history of the journal, and that the present editor of the journal is Keith Porter's scientific grandson. Porter's account (with H. Stanley Bennett) of the founding of the journal appeared in the December 1981 supplement *Discovery in Cell Biology* (*Journal of Cell Biology*, Vol. 91, No. 3, Pt. 2).

In 1961, Porter moved to Harvard University to become Professor of Biology and subsequently Chairman of the department. In 1968, he moved to the University of Colorado at Boulder as Chairman of the new Department of Molecular, Cellular, and Developmental Biology. There he developed facets of scanning microscopy and he established a High Voltage Electron Microscope Facility that continues to be a national resource. From each instrument he employed, he drew a set of compelling images that he disseminated in talks, publications, and atlases. He retired from the University of Colorado in 1983, at which time the building that housed his laboratory was named in his honor. He did not rest on his laurels but moved again to become Wilson Elkins Distinguished Professor in the Department of Biological Sciences at the University of Maryland, Baltimore County. At age 75, he finally moved once again to become Distinguished Research Professor of Biology at the University of Pennsylvania, returning to collaborate with Lee Peachey, who was his first graduate student. His interest in students was whetted at The Rockefeller University, where he and Palade established a premier course in comprehensive cell biology. At Rockefeller, Harvard, Colorado, and Maryland, he trained a coterie of postdoctoral associates and graduate students who spread the gospel of cell biology and fine structure throughout the world. While he had a pungent wit, a sharp sense of humor, and a critical eye, for which his lectures were known, many a cell biologist throughout the country owes his/her position to Keith Porter's kind recommendations and sympathetic encouragement. Even now, he continues to sup-

port the field through the Keith Porter Endowment to which his estate is the major contributor.

Porter was celebrated and honored in many ways, with festschrifts, with a dedicated volume of the *Journal of Cell Biology* (Palade, 1977), and with a number of important prizes. Among his other honors, he was a member of the National Academy of Sciences, a corecipient with George Palade and Albert Claude of the Louisa Gross Horwitz Prize, and a corecipient with Palade and Daniel Mazia of the first E.B. Wilson Award of the American Society for Cell Biology. The Porter Lecture, named for him, is the premier lecture at the annual meeting of the society. The Nobel prize, presented in 1974 for work in which he pioneered, eluded him. In 1977, Porter received the National Medal of Science from President Carter.

In 1956, as preface to the Proceedings of a Conference on Tissue Fine Structure that appeared as a supplement to Volume 2 of this journal, Porter wrote: "It must be evident by now to even the most confirmed skeptic that electron microscopy is destined to have a profound influence on the future development of biology and related sciences. Investigations carried on with the microscope . . . are currently revealing unexpectedly numerous and complex details of structure in the cells of plants and animals. Such studies usher in a period of microscopic discovery that will surely match if not surpass in importance the 40 or 50 years of activity that followed the introduction of improved optical microscopes, and techniques of fixation, sectioning, and staining about a century ago.

For those of us who are fortunate to be part of this new development, these are days of great interest and opportunity."

The 40 years have passed and now the father of the field has died. We would do well to leave our successors as rich a legacy of opportunity in cell biology as he has left us.

#### References

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#### Peter Satir

*Department of Anatomy and Structural Biology, Albert Einstein College of Medicine, Bronx, New York 10461-1602*